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AGGREGATED COLONIES IN MADREPORARIAN CORALS.

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PROF. G. VON KOCH,[1] in the eighth of his well-known "Kleinere Mittheilungen über Anthozoen," describes what he terms "Aggregated Colonies" as occurring in the simple Mediterranean coral, *Balanophyllia verrucaria*. The designation "aggregated" is employed by the author for such colonies as have been formed through the secondary fusion of individuals which were originally distinct, thus distinguishing them from most other Anthozoan colonies which are produced by the budding or fission of a single individual.

Von Koch collected around the small island of Vivara in the Mediterranean Sea a number of Balanophyllia which, instead of retaining the simple habit usual for this genus, consisted of two or more polyps. The corallites were fused with one another and possessed a common base, and many of the septa of adjacent calices were continuous. The tentacular system of each individual polyp was distinct, a mouth occurred in the center of each oral disk, but the column wall passed uninterruptedly from one polyp to another.

An examination of serial transverse sections of the corallum of two such colonies revealed that the corallites were independent towards the base, but united in a common secondary skeletal formation. In the case of a colony constituted of two individuals, one much larger than the other, von Koch concludes that the union had arisen through a larva settling near an older polyp; after the first skeletal rudiments were formed their coralla became fused through secondary deposition of calcareous matter, the larger polyp contributing most.

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[1] Koch, G. von. Kleinere Mittheilungen über Anthozoen. VIII. Aggregirte Kolonien von Balanophyllia verrucaria Aut. *Morph. Jahrb.*, vol. xviii.

Sections of another colony, composed of four individuals, showed that the four corallites remained at approximately the same proportional size throughout, and the writer assumes that the mass was formed by four larvæ which settled close to one another and practically at the same time, each constructing its own corallum, and contributing an equal share to the formation of the common investing skeleton.

The late Prof. H. de Lacaze-Duthiers[1] has recently given an account of somewhat similar aggregations of the simple coral Caryophyllia, obtained from Port-Vendres. On many of the larger corallites smaller examples were growing, in such a way as to leave little doubt that the "bouquet" was a result of the adherence of Caryophyllia larvæ to the corallum of a polyp already established. Occasionally the individual members of a colony are polyps of practically equal size, as if originating from larvæ which settled simultaneously and in close proximity. In most of the examples described and figured by Lacaze-Duthiers the corallites retain their individuality, without the formation of a common secondary skeletal mass, but in one specimen (*loc. cit.*, Pl. XV, Fig. 12) two calices appear to have fused at their margin.

Prof. C. Schuchert has drawn my attention to the colonial condition generally exhibited by the rugose coral, *Streptelasma* (*Palæophyllum*) *divaricans* (Nicholson).[2] Representatives of the genus Streptelasma are usually simple, but numerous specimens of the above species in the collections of the United States National Museum, collected from near the top of the Lower Silurian of Ohio, constitute small colonies of two to six individuals. The colonies were at first supposed to have been formed "by lateral gemmation, or rarely by fission," but a close examination shows that such an explanation is very improbable. Each member retains more independence of form than is usual in colonies produced by gemmation or fission. In many instances two or more corallites are found adhering to some foreign object, such as a shell of *Rhynchotrema capax* or a monticuliporoid bryozoan. The corallites of the different colonies vary greatly in size, but the members of any colony are practically equal, showing them to be derived from polyps of a similar age; there is no suggestion of a larger parent corallite and smaller buds. They seem best regarded as aggregated colonies.

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[1] Lacaze-Duthiers, H. de. Les Caryophyllies de Port-Vendres, *Arch. de Zoöl. Exp. et Gen.*, Ser. 3, vol. vii, 1899.

[2] Geol. Surv. Ohio, Pal. 11, 1875, p. 220, Pl. XXII, Figs. 10, 10 *b*.

The common West Indian coral, *Siderastræa radians* (Pallas), in the course of its development, has recently provided me with actual instances of colony formation by the fusion of originally free, distinct larvæ. The process of growth has been followed from the time of fixation of the free-swimming individuals as far as the production of the early skeleton.

Small, unfixed, adult colonies of *S. radians* occur in plenty in the shallow waters of Kingston harbor, Jamaica, and are easily kept alive in aquaria in the laboratory. The physiological activity of numbers of unicellular algæ, symbiotic within the endodermal tissues, renders unnecessary any artificial means of aëration of the water. Colonies are occasionally met with in which the internal cavity of many of the polyps is crowded with larvæ. These are shot out from time to time and are thus free to establish new colonies in turn. As a rule, only one or two larvæ are extruded at a time, but upon disturbance of a fully charged colony a score or so would appear together. In one colony the intermittent liberation of fresh individuals was continued for about a month.

Immediately on being set free within the water the larvæ were able to swim about, and revolved around their principal axis, being provided with a uniform layer of cilia. They measured two to three millimeters in length and were mostly pear-shaped, the narrow aboral end being anterior, or forward, in swimming. The broad oral end was posterior and dark colored, the latter condition owing to the presence of zoöxanthellæ (yellow cells) within the outer ectoderm. In a few larvæ the forward aboral end was the broader, as appears to be more usually the case in actinian and madreporarian larvæ when first extruded. The majority were opaque, without any outward indication of internal mesenteries, but occasionally a distended specimen was met with in which the walls were nearly transparent and revealed eight internal mesenterial divisions.[1]

During the first day the Siderastræa larvæ remained near the surface of the water or gathered around the sides of the vessels in which the colonies were kept. Afterwards they traversed the water as a whole, though some preferred the neighborhood of the bottom of the vessel. From the first day many would sink to the bottom and there lie motionless for a time, after which the swimming movements might recommence.

By the evening of the second day a few individuals had fixed themselves permanently, either to the sides or bottom of the vessels, or to the foreign objects partly incrusted by the parent colonies. At first the larvæ would adhere by means of the actual tip of the narrow extremity, but this would soon flatten out and form a broad base, a small rounded oral aperture appearing at the free extremity. Whether or not any individual larva would settle seemed very uncertain, for out of several hundreds set free comparatively few became permanently fixed. If fixation were not accomplished within the first few days it seemed to be impossible afterwards. In one instance about a score of larvæ were isolated, and nearly all kept alive for a period of twenty days, without any of the specimens settling, although various suitable objects were placed in the vessels.

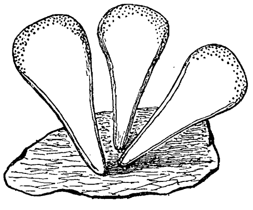

FIG. 1.

While many larvæ fixed themselves isolated from others, a decided disposition to settle simultaneously in small groups was evident. Thus in Fig. 1, where three larvæ are represented, all in the first stage of fixation, their narrow apices are so close as to be nearly touching. It is clear that when they flatten out by this extremity their walls will be in close contact, and a colony of three young polyps will result.

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[1] The larvæ of West Indian corals are usually set free at a stage at which three or more pairs of mesenteries are already developed, the stomodæum fully formed but non-functional, and the interior wholly, or in part, occupied by a highly vacuolated tissue. After liberation the stomodæum becomes functional, the larva enlarges, its walls become more transparent, and much of the vacuolated tissue breaks down and is seen to be extruded at intervals through the oral aperture.

Such a colony, adherent to a pebble, and formed of seven individuals, is represented in Fig. 2. The drawing was made two or three days after fixation of the larvæ, when the adult polypal form was beginning to be assumed, and the tentacles were just appearing as rounded prominences. All the polyps are at practically the same stage of development, proving that they settled synchronously, or nearly so. They are irregularly arranged with regard to one another, and in their effort to fully expand the walls press upon one another, and produce distortion of the proximal part of the column.

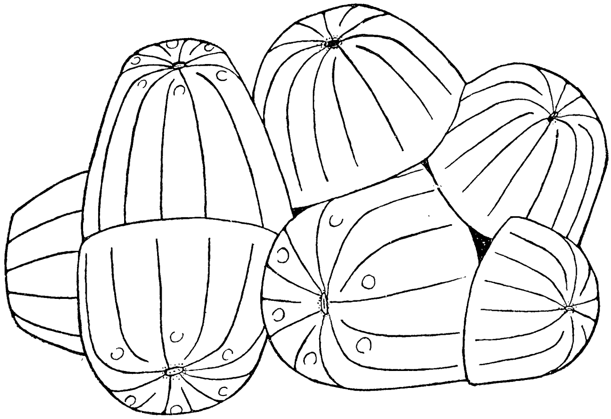

FIG. 2.

To the under surface of another small pebble thirty-eight larvæ attached themselves in groups of two, three, or more. One of these groups contained a dozen or so young polyps, all touching, the mutual pressure producing an angulation of the normally circular base. Another group of thirty-two became adherent during a single night to the surface of a small glass dish. In this case nearly all the members, upon flattening, were touching to a greater or less degree.

Fixation having taken place, the larvæ, now to be regarded as polyps, seemed remarkably vigorous, and underwent the next stages of development with comparative rapidity. In sharp contrast with this the unfixed larvæ remained all the time at practically the same stage as when first extruded.

The glass vessel to which some of the polyps became adherent was broken into small fragments, with the polyps still upon them. These could then be transferred from one aquarium to another, or examined in small dishes as transparent living objects under the microscope. In this way the growth of the various organs was followed day by day. Some specimens were kept alive for a period of seventeen weeks, the development of the tentacles and septa being followed as far as the third cycle. For the present purpose the normal development will be succinctly reviewed, so as to compare the modifications introduced as a result of the primary grouping of many of the polyps in colonies.

On fixation the tissues of the polyps became transparent and the six pairs of primary mesenteries were seen to be already present, four pairs attached to the stomodæum and two pairs incomplete. About a month elapsed before the members of the second cycle began to appear, being first represented by a pair in each of the dorsal exocœles, then later by a pair in each of the middle exocœles, and finally by a pair in each ventral exocœlic chamber.

The first tentacles commenced to make their appearance two or three days after settling, as six rounded outgrowths over alternate mesenterial chambers, and early showed an opaque, white, knob-like apex distinct from a short, more transparent stem. The six prominences appeared simultaneously, constituting a first cycle, and were equal in size and distance apart, and in communication with the exocœlic chambers. About four weeks passed before another cycle of six tentacles appeared, internal to the first, and situated over the entocœlic chambers. The further tentacular development was somewhat complicated and need not be here considered.

Three or four days after fixation the skeleton was first observed in the form of six radiating septal upgrowths, practically equal in size. At the same time a narrow peripheral calcareous ring was formed, its outer surface uncovered by the soft polypal tissues, and therefore to be regarded as an epitheca.

The six septa were free from one another and from the epitheca, and situated at equal distances apart within the primary entocœlic chambers, thus alternating with the cycle of six exocœlic tentacles first to arise.

A day or two after the formation of the first cycle of entosepta the six exocœlic septa began to make their appearance, in some cases simultaneously, but successively in others, in bilateral pairs from the dorsal to the ventral aspect of the polyp.

Under ordinary transmitted light no basal skeletal formation could be detected, but with polarized light the presence of crystalline particles could be demonstrated. In polyps macerated at this period a very thin basal disk was recognizable, formed of an aggregation of irregular granules, and continued at its edge as the upturned epitheca, the six or more radial septa arising from it vertically some distance within.

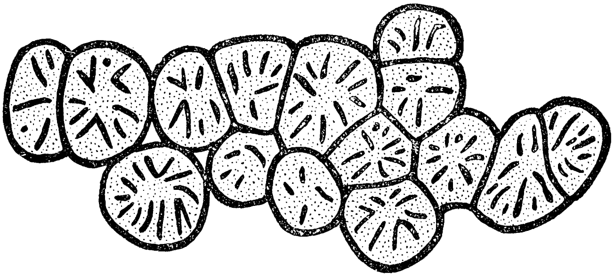

FIG. 3.

A wide range of variation was exhibited by the different polyps as to the rate of growth of the various organs, especially in the later stages. The individuals which were larger on fixation soon outstripped the others; scarcely any succumbed, and it was possible to feed them on fragments of worms and mollusks.

Such a regular, symmetrical development was characteristic only of the isolated polyps, free to expand equally on all sides. The polyps in groups were crowded to such a degree as to necessitate arranging themselves at all angles with regard to one another and the incrusted object. Sometimes part of the base of one polyp would be reclining against part of another; but none of the individuals seemed to be overpowered by such close proximity. As a whole, the growth of the colonial polyps was much less forward than that of the isolated specimens. All were normal as regards the occurrence of the six pairs of primary mesenteries—four complete and two incomplete; the tentacles also were represented by a primary cycle of six exocœlic representatives and a secondary inner cycle of six entocœlic members. Variations and irregularities, however, were introduced in connection with the formation of the skeleton. The epitheca was invariably produced at the free basal edge of the column wall, and under such conditions as those represented in Fig. 2, it is clear that its outline would be irregular, and that the epitheca of one polyp would be in contact with that of the contiguous polyps to the extent the polypal walls were adherent. Likewise the basal disks of two polyps reclining against one another would be formed at a sharp angle.

The septa of the colonial polyps exhibited from the beginning many irregularities and imperfections. Such a series is indicated in Fig. 3. The drawing was taken from the under surface of a living colony of seventeen polyps, adherent to a fragment of glass, and viewed by transmitted light, so that only the basal skeletal structures are exhibited. The polyps are seen to vary greatly in size; the outline is angulated where they are in contact with others, and rounded on the free border. The two larger polyps at each extremity of the colony partly overlap one another at an angle, though this is not very obvious from their flat basal expansions alone. The thickened margin to each polyp represents the epitheca, that of two contiguous polyps being fused along the line of contact. The basal disk is yet so thin as to be practically transparent and is indicated by the dotted areas.

The radiating dark bands, as a rule simple, but sometimes forked, represent the adherent surface of the septa; the latter on account of their vertical thickness are non-transparent like the epitheca. In no polyp are the two orders of six septa fully or regularly developed in the manner already described for isolated polyps. Any number of septa from four to twelve are represented, as a rule with a suggestion of alternating large and small members.

The development of the colonial polyps was not followed far beyond the stage represented in Fig. 3. Growth was very slow compared with that of the isolated individuals, and most were preserved for further study. There was no indication, however, but that under favorable natural conditions the aggregations would have grown into fully mature colonies. In the later stages the primary irregularities due to crowding would probably have been outgrown, and the groups would then present all the characters of normal colonies arising by budding.

In one feature the polyps constituting an ordinary colony of *S. radians* differ from those in a colony formed of aggregated, primarily independent units. Polyps arising by gemmation are, as a rule, only incompletely cut off from the parent; their internal cavities are from the beginning in communication with those of the adult polyps, so that the nutrient fluid can circulate from one individual to another. Such would not be the case at first with aggregated colonies, and at the very early stage at which the observations on Siderastræa were made I could not assure myself that intercommunication was established. The intervening external epitheca would for some time interfere with such a possibility, but no doubt this structure, along with the basal plate, would be left behind in the upward growth of all except the marginal polyps. For, except a most rudimentary formation at the margin, the epitheca is absent from mature colonies.

It does not seem probable that the phenomenon of aggregated colonies is a prominent feature of coral growth. Still, it is necessary that its possibility should be recognized, for wherever it occurs the resulting colony will probably differ somewhat from one produced by normal budding or fission, while when occurring in usually simple corals its non-recognition might lead to disastrous results.

All students of both fossil and recent corals are familiar with the fact that very often simple coralla are found adhering to the dead portions of colonies, undoubtedly the young of these. Among West Indian corals the occurrence of young polyps under such conditions is very frequent in *Manicina areolata*

(Linn.) and *Favia fragum* (Esper). A colony of Manicina will sometimes possess five or six adhering young polyps, the different members of which exhibit one, two, three or more oral apertures, and in other ways are regularly developed. Their structural details prove that they have originated not by fission or budding, but from larvæ which have settled, probably immediately or shortly after extrusion, in close association with the parent colony. Colonies of Manicina and Favia are often found charged with larvæ, and their extrusion has been frequently observed.

Much variation exists as to the activity displayed by the larvæ of these and other coral species immediately on extrusion. In some cases the larvæ are quite vigorous, and able to swim about from the beginning; and under natural conditions these would no doubt continue their activities for a long time, and might be drifted great distances before settling. Others again sink immediately on liberation from the interior of the parent, and falling upon the nearest object may settle there. In most instances the nearest object will be the dead lower part of the parent colony. It is thus easy to see how, under ordinary natural conditions, such aggregations as those found by von Koch and Lacaze-Duthiers may have arisen. The grouping of the larvæ in *S. radians* appeared to be less fortuitous than this, for practically all the specimens were able to swim about immediately on being set free. It may be that the tendency towards aggregation above described was in some way influenced by the cramped artificial conditions of the small aquaria.

The possibility of extruded larvæ settling in numbers immediately around the parent, instead of drifting widely apart, is a phenomenon likewise to be looked for in the field study of the closely allied Actiniaria. On the coral reefs in West Indian waters occur large irregular patches, often several feet across, of one or other of the anemones, *Actinotryx sancti-Thomæ* Duch. & Mich. and *Ricordea florida* Duch. & Mich. The polyps are usually adherent to some dead coral slab, and in a single patch there may be hundreds of individuals. Both species exhibit asexual reproduction by fission, and in any group are to be found specimens with from one to three or more oral apertures on a single disk. One may assume that all the individuals constituting a patch have arisen asexually from one or a few primary polyps. But such does not appear to be the case. Aggregations have been observed in which one large example would be surrounded by a number of others, all smaller but practically uniform in size. Both species are found to extrude larvæ very freely, and there seems no doubt that the patches are in the main formed of individuals derived from such larvæ as settled near the parent. A certain number of fission polyps would also be expected. Externally it would be practically impossible to distinguish between larval polyps and fission polyps, but the internal mesenteries afford distinctive characters as to the one or the other form.

Similar extensive patches of the large discosomid, *Stoichactis helianthus* (Ellis) are not infrequent. Their occurrence is probably to be explained in the same manner as above, that is, as due almost entirely to the aggregation of distinct larvæ. Asexual reproduction seems to be very rare in this species.

Polyps of the northern species of Metridium usually occur in groups. From the researches of G. H. Parker[1] and others, asexual reproduction seems to play a considerable part in the crowding habit of these, but the possibility of aggregating larvæ also should not be overlooked, even though *M. marginatum* extrudes unfertilized eggs.

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[1] Parker, G. H. Longitudinal Fission in Metridium marginatum Milne-Edwards, *Bull. Mus. Comp. Zoöl. Harvard*, vol. xxxv, 1899.